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TROPICAL FERN HOSTS OF RUST FUNGI

J. H. FAULL

RUSTS ON FERNS are referred in current literature on mycology and plant pathology to the definitive genera Hyalopsora, Milesia, Uredinopsis, Desmella and Puccinia and in a few instances to the imperfect genus Uredo. The complete life-histories of many species of the first three have already been determined experimentally; in all cases they have proved to be heteroecious, with species of Abies serving exclusively as their aecial hosts. So it may quite safely be assumed that the same pattern is potentially true of all the other species of Hyalopsora, Milesia and Uredinopsis. Regarding Desmella, uredia and telia only are known; and as they are so unlike those of the three foregoing genera, the identities of hosts that can carry the aecial stages of *Desmella* rusts are not even conjectured. It is a strange genus, taxonomically standing quite apart from the other fernrestricted genera. Thus far it has been reported from the American tropics only. Among the remaining fern rusts, a single species of *Puccinia* has been described, though solely with respect to its uredia and telia. Finally, as to the Uredo fern rusts, they can with reasonable certainty be recognized as uredo stages of one or other of the five definitive genera. Indeed, not a few of the named species of these genera have been described from the uredo stage and without knowledge of telia. Although technically open to some objections, this practice does offer advantages if used with discretion. With possible exceptions of Australia and Tasmania, fern rusts are world-wide in distribution. Of course, locally within any extensive region there may be limiting factors, such, for example, as continuously high day and night temperatures. Otherwise they are likely to be found wherever ferns grow and on a surprisingly large number of specific hosts. Naturally, where those that are Abies-infecting occur beyond the ranges of Abies, they can be perpetuated solely by seasonal transmission from affected ferns to plants of identical kind or of species that are likewise susceptible. Indeed, as the southern distributional limits of Abies are approached, this method becomes increasingly frequent, even in those rust species that lack amphispores. Of course this method is possible for amphispore-producing rusts in any latitude, but otherwise only wherever there is a sufficiently close overlapping of successive seasonal crops of fronds, that is, a succession within the vital life-span of ordinary urediospores. It may not be superfluous to recall to mind here that the most southerly ranges of existing Abies, though well within the tropics in the western hemisphere and reaching to the tropics in the eastern, fall far short of the equator.

310 JOURNAL OF THE ARNOLD ARBORETUM [vol. xxviii TABLE I PUBLISHED TROPICAL FERN HOSTS, THEIR RUSTS AND REGIONAL ORIGINS

Fern hosts	Rusts	Regional origins	
1. Adiantum andicola Liebm.	Uredinopsis investita Faull	Guatemala [†]	
2. Anemia fulva (Cav.) Sw.	Desmella Aneimiae (Henn.) Syd.	Brazil	
3. Anemia Phyllitidis (L.) Sw.	Desmella	Brazil	

- 4. Anemia tomentosa (Sav.) Sw. Desmella Aneimiae (Henn.) Syd. Brazil† (A. cheilanthoides Kaulf.) 5. Antrophyum lanceolatum (L.) Dominican Hyalopsora Polytaenii (KCT) Republic[†]; Kaulf. Cummins Porto Rico 6. Blechnum occidentale L. Milesia australis Arthur Colombia†; Costa Rica; Porto Rico 7. Blechnum unilaterale Sw. Uredinopsis Mayoriana Diet. Colombia† [B. blechnoides (Lagerh.) C.Chr.] 8. Blechnum volubile Kaulf. Desmella (Uredo blechnicola Brazilt Henn.)
- 9. Cheilanthes pyramidalis Fée Uredinopsis glabra Faull Mexico
 10. Coniogramme fraxinea (Don) Milesia Coniogrammes (Hirats. Formosa

Diels	f.) n. comb. (Milesina Conio- grammes Hirats. f.)	rormosa
11. Cystopteris fragilis (L.) Bernh.	Uredinopsis glabra Faull	Mexico†
12. Dennstaedtia rubiginosa (Kaulf.) Moore	Desmella	Porto Rico
13. Dennstaedtia rubiginosa (Kaulf.) Moore	Milesia Dennstaedtiae (Diet.) Faull	Colombia†
 14. Dryopteris sp. [Close to D. oligocarpa (H. & B.) Kuntze] 	Milesia andina Faull	Ecuador†
15. Dryopteris Clarkei (Bak.) Kuntze	Milesia Miyabei (Kamei) Faull	Formosa
16. Dryopteris dentata (Forsk.) C. Chr.	Desmella	Porto Rico

- [D. mollis (Jacq.) Hieron.]
- 17. Dryopteris patens (Sw.) Milesia consimilis Arthur Jamaica† Kuntze
- 18. Dryopteris Poiteana (Bory) Desmella Urban
- 19. Dryopteris Poiteana f. proli- Desmella fera

Porto Rico

Venezuela

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TABLE I (Continued)

	Fern hosts	Rusts	Regional origins
20.	Dryopteris quadripinnata Hayata	Milesia carpatica var. erythrosora Faull [Milesina erythrosora (Faull) Hirats. f.]	Formosa
21.	Dryopteris tetragona (Sw.) Urban	Desmella	Porto Rico
22.	Dryopteris tetragona var.	Desmella	Venezuela

- opients retragona val. guadalupensis C.Chr.
- 23. Elaphoglossum sp.
- 24. Elaphoglossum latifolium (Sw.) J. Sm.
- 25. Lygodium micans Sturm (Lygodium sp.)
- 26. Lygodium polymorphum (Cav.) HBK
- Puccinia Lygodii (Hariot) Arthur

Milesia philippinensis (Syd.)

n. comb. (Milesia tenuis Faull)

27. Lygodium volubile Sw.

- 28. Nephrolepis cordifolia (L.) Presl
- 29. Nephrolepis pendula (Raddi)

- Colombia Hyalopsora obovata (Arthur) Cummins
- Jamaica† Hyalopsora obovata (Arthur) Cummins
- Br. Guiana Uredo (Milesina Lygodii Syd.)

Brazil†; San Salvador; Trinidad; Venezuela Brazil Philippine Islands†

Uredo

- Colombia[†] Milesia columbiensis (Diet.) Arthur J. Sm.
- 30. Nephrolepis rivularis (Vahl) Milesia insularis Faull Porto Ricot Mett.
- Milesia Cryptogrammes (Diet.) Philippine 31. Onychium japonicum Islands n. comb. [Milesina Crypto-(Thunb.) Kunze (Cryptogrammes (Diet.) Hirats. f.] gramme japonica Prantl)
- 32. Pellaea cardiomorpha Weath. Uredinopsis glabra Faull Mexico
- 33. Pellaea ternifolia (Cav.) Link Hyalopsora Cheilanthis (Peck) Ecuador Arthur
- (von Thü- Madagascar 34. Pellaea viridis (Forsk.) Prantl Milesia nervisequa men) Faull [Pellaea hastata (Thunb.) Prantl]
- Ecuador[†]; 35. Pityrogramma calomelanos Desmella Venezuela (L.) Link Ecuador 36. "Polypodiacea sp." Desmella
- Milesia Hashiokai (Hirats. f.) Formosat 37. Polypodium arisanense Hayn. comb. (Milesina Hashiokai ata
 - Hirats. f.)
- 38. Polystichum amabile (Bl.) J. Sm.
- Milesia arisanensis (Hirats. f.) Formosa[†] n. comb. (Milesina arisanense Hirats. f.)

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TABLE I (Continued)

Fern hosts	Rusts	Regional origins
39. Pteridium aquilinum (L.) Kuhn, including varieties and marginal species	Uredinopsis macrosperma (Cooke) Magn.	Brazil; Colombia; Cuba; Guatemala: Honduras; Jamaica; Mexico:

Mexico; Panama; Venezuela; Belgian Congo†

40. Pteridium aquilinum var. de- Uredinopsis aspera Faull Hawaii compositum (Gaud.) Tryon

41. Pteridium aquilinum var. Uredinopsis Hashiokai Hirats. f. Formosa† Wightianum (Agardh) Tryon

†Where type was collected.

Not much collecting of fern rusts has been done in the tropics. Yet there is a considerable accumulation from mainly incidental collecting over the years. These are listed above in Table I, and it is quite an impressive compilation. But my own limited, yet intensive collectings in the tropics of North America, supplemented by occasional contributions from correspondents and a few gleanings from fern collections in the Gray Herbarium of Harvard University, are sufficient to show that the number of known fern hosts is probably a small representation of fern species that. in one region or another, carry rust fungi. Table II presents new acquisitions obtained by me in the ways indicated above. Among these are unpublished collecting records of a few species listed in Table I; they are marked with an asterisk (*). One of the reasons for publishing these lists before detailed studies have been completed on them is to call the attention of collectors in the tropics to a seemingly passed-by group of rust hosts. They will also serve to indicate that our knowledge of fern and fir rusts is far from complete. But now at least enough materials and sources of supply are available to justify more adequate taxonomic review and a wider range of other investigations.

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TABLE II

NEW RECORDS FOR TROPICAL FERN HOSTS OF RUST FUNGI

Fern hosts	Rusts	Regional origins
А.	Fam. Ophioglossaceae	
1. Botrychium virginianum (L. Sw.) Hyalopsora	Guatemala

B. Fam. Schizaeaceae

2. Anemia hirsuta (L.) Sw.

3. Anemia hirsuta (L.) Sw.

4. Lygodium heterodoxum Kunze

5. Gleichenia sp. (?)

6. Cyathea sp.

7. Cyathea fulva (M. & G.) Fée

8. Cyathea Harrisii Underw.

9. Cyathea mexicana Schl. & Cham.

Desmella

Milesia

Uredo

C. Fam. Gleicheniaceae (?) Milesia D. Fam. Cyatheaceae

> Hyalopsora Milesia Milesia Milesia

Jamaica; Mexico Jamaica; Mexico Guatemala

New Guinea

New Guinea Mexico Jamaica Guatemala

E. Fam. Polypodiaceae

10. Adiantum Capillus-veneris L. Hyalopsora Desmella 11. Adiantum latifolium Lam. 12. Adiantum subcordatum Sw. Hyalopsora Hyalopsora 13. Anogramma chaerophylla (Desv.) Link 14. Anogramma chaerophylla Uredinopsis (Desv.) Link Milesia 15. Asplenium malayo-alpinum Holtt. 16. Asplenium monanthes L. Hyalopsora 17. Asplenium monanthes var. Hyalopsora Galeotti (Fée) Hieron. Hyalopsora 18. Athyrium sp. 19. Athyrium Dombei Desv. Uredinopsis

Mexico Trinidad Brazil Mexico Mexico New Guinea Guatemala; Mexico Mexico New Guinea Guatemala; Mexico Mexico

- 20. Athyrium paucifrons C. Chr. Milesia (?)
- 21. Athyrium Skinneri Moore
- 22. Blechnum sp.
- Milesia 23. Blechnum fraxineum Willd.

Hyalopsora Milesia or Hyalopsora Mexico New Guinea Venezuela

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TABLE II (Continued)

Fern hosts	Rusts	Regional origins
24. Blechnum occidentale L.*	Milesia	Cuba; Guatemala;
		Jamaica;
		Mexico;
		Panama;
		Venezuela

25. Blechnum orientale L. Hyalopsora 26. Blechnum unilaterale Sw. Milesia 27. Cheilanthes membranacea Uredinopsis (Davenp.) Maxon 28. Cheilanthes microphylla Sw. Milesia 29. Cheilanthes pyramidalis Fée Hyalopsora 30. Cheilanthes tenuifolia Milesia (Burm.) Sw. 31. Coniogramme fraxinea (Don) Hyalopsora Diels

- 32. Cyclopeltis semicordata (Sw.) Desmella J. Sm.
- 33. Cystopteris fragilis (L.) Hyalopsora Bernh.
- 34. Dennstaedtia adiantoides (H. Milesia & B.) Moore

Borneo Mexico Mexico Jamaica Mexico New Guinea China (Lat. 25° N) Trinidad Mexico

Cuba

- 35. Dennstaedtia cicutaria (Sw.) Milesia Moore
- 36. Dennstaedtia dissecta (Sw.) Milesia Moore
- 37. Dennstaedtia exaltata (Kze.) Milesia Hieron.
- 38. Dennstaedtia ordinata (Kaulf.) Moore

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- 39. Dennstaedtia rubiginosa (Kaulf.) Moore*
- 40. Dennstaedtia rubiginosa (Kaulf.) Moore*
- 41. Diplazium sp. (?) 42. Diplazium sp. (?) 43. Diplazium crenulatum
- O. Liebm.

Desmella

Milesia

Milesia

Hyalopsora Hyalopsora Milesia

Mexico

Jamaica Mexico

Jamaica

Jamaica

Guatemala; Jamaica; Panama New Guinea New Guinea Guatemala

- 44. Diplazium expansum Willd. Desmella
- 45. Dryopteris sp. Milesia
- 46. Dryopteris, n. sp. (?) acc. to Milesia Maxon
- 47. Dryopteris boqueronensis Milesia Hieron. (?)

Cuba New Guinea Jamaica

Ecuador

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TABLE II (Continued)

Fern hosts	Rusts	Regional origins
48. Dryopteris concinna (Willd.) Kuntze	Milesia	Guatemala; Panama
49. Dryopteris dentata (Forsk.) C. Chr.	Milesia	Panama
50. Dryopteris diplazioides (Desv.) Urban	Milesia	Ecuador

- 51. Dryopteris effusa (Sw.) Milesia Urban
- 52. Dryopteris equestris (Kunze) Milesia C. Chr.
- 53. Dryopteris firma (Baker) Milesia C. Chr.
- 54. Dryopteris heteroclita (Desv.) Milesia C. Chr.
- 55. Dryopteris melanochlaena Milesia C. Chr.
- 56. Dryopteris navarrensis Christ Milesia
- 57. Dryopteris Nockiana (Jenm.) Milesia C. Chr.
- 58. Dryopteris oligocarpa (H. & B.) Kuntze
- 59. Dryopteris oligocarpa (H. & B.) Kuntze

Milesia

Desmella

Jamaica Guatemala Jamaica Guatemala Jamaica Jamaica 315

- 60. Dryopteris opposita (Vahl) Milesia Urban (?)
- 61. Dryopteris paleacea (Sw.) Milesia C. Chr.
- 62. Dryopteris patens (Sw.) Milesia Kuntze*
- 63. Dryopteris patula (Sw.) Un- Milesia derw. var. Rossii C. Chr.
- 64. Dryopteris pilosula (Kl. & Hyalopsora Karst.) Hieron. (approaches D. navarrensis Christ)
- 65. Dryopteris resinifera (Desv.) Desmella Weatherby
- 66. Dryopteris resinifera (Desv.) Milesia Weatherby
- 67. Dryopteris rubigena Maxon Milesia & Morton

Jamaica ; Mexico Panama

Guatemala; Mexico Jamaica

Mexico

Guatemala

Mexico

Guatemala

Guatemala

- 68. Dryopteris rudis (Kze.) Milesia C. Chr. (?)
- 69. Dryopteris Sloanii (Bak.) Milesia Kuntze (D. oligophylla Maxon)

Guatemala

Jamaica

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TABLE II (Continued)

Fern hosts	Rusts	Regional origins
70. Dryopteris Sprengelii (Kaulf.) Kuntze	Milesia	Jamaica
71. Dryopteris tetragona (Sw.) Urban*	Desmella	Jamaica
72. Elaphoglossum lingua (Rad- di) Brack.	Hyalopsora	Jamaica

73. Elaphoglossum Pringlei (Da- Milesia venp.) C. Chr.

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- 74. Hemionitis palmata L.Milesia75. Odontosoria Jenmanii Maxon Milesia
- 76. Pellaea cardiomorpha Weath- Hyalopsora erby
- 77. Pityrogramma sulphurea Desmella (Sw.) Maxon
- 78. Polybotrya osmundacea HBK Milesia
 79. Polypodium aureum L. Desmella
 80. Polypodium ellipsoideum Fée Hyalopsora
- 81. Polypodium fissidens Maxon Hyalopsora
 82. Polypodium fissidens Maxon Milesia
 83. Polypodium loriceum L. Desmella
 84. Polypodium Martensii Mett. Hyalopsora

Mexico Jamaica Jamaica Mexico Jamaica Jamaica Panama Guatemala; Mexico Guatemala Guatemala Jamaica Guatemala; Mexico Guatemala; Mexico China (Lat. 26° N) Guatemala Jamaica Jamaica Panama Jamaica New Guinea

- 85. Polypodium plesiosorum Uredinopsis Kunze
- 86. Polypodium Veitchii Bak. var. Hyalopsora glaucopsis (Franch.) Ching
- 87. Polystichum rachichlaena Fée Milesi
 88. Pteris longifolia L. Milesi
 89. Pteris longifolia L. Desmi
- 90. Pteris quadriaurita Retz. 91. Pteris quadriaurita Retz.
- 92. Tectaria irregularis (Pr.) Copeland (?)
- 93. Woodsia mollis (Kaulf.) J. Sm.

Milesia Milesia Desmella Desmella Milesia

Hyalopsora

Mexico

SUMMARY AND COMMENTS

1. Rusts are recorded for the first time as occurring in the Ophioglossaceae and Cyatheaceae. To these may possibly be added the Gleicheniaceae.

2. *Hyalopsora* rusts are recorded for the first time as occurring in the Ophioglossaceae and Cyatheaceae.

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3. *Milesia* rusts are correctly recorded for the first time as occurring in the Schizaeaceae and Cyatheaceae. To these may possibly be added the Gleicheniaceae.

4. Species of the following fern genera, found growing within the tropics, are recorded in this paper as:

(a) hosts for DESMELLA rusts: Adiantum (1), Anemia (4), Blechnum (1), Cyclopeltis (1), Dennstaedtia (1), Diplazium (1), Dryopteris (5), Pityrogramma (2), "Polypodiacea" (1), Polypodium (2), Pteris (2); (b) hosts for HYALOPSORA rusts: Adiantum (2), Anogramma (1), Antrophyum (1), Asplenium (1), Athyrium (2), Blechnum (1), Botrychium (1), Cheilanthes (1), Coniogramme (1), Cyathea (1), Cystopteris (1), Diplazium (2), Dryopteris (1), Elaphoglossum (2), Pellaea (2), Polypodium (4), Woodsia (1); (c) hosts for MILESIA rusts: Anemia (1), Asplenium (1), Athyrium (1), Blechnum (4), Cheilanthes (2), Coniogramme (1), Cyathea (3), Dennstaedtia (6), Diplazium (1), Dryopteris (26), Elaphoglossum (1), Gleichenia ? (1), Hemionitis (1), Nephrolepis (3), Onychium (1), Odontosoria (1), Pellaea (1), Polybotryum (1), Polypodium (2), Polystichum (2), Pteris (2), Tectaria (1); (d) hosts for UREDINOPSIS rusts: Adiantum (1), Anogramma (1), Asplenium (1), Athyrium (1), Blechnum (1), Cheilanthes (2), Cystopteris (1), Pellaea (1), Polypodium (1), Pteridium (including under P. aquilinum its varieties and marginal species).

The names in black face are genera within the tropics recorded for the first time as hosts for rust fungi. The numbers of species reported for each genus are indicated in parentheses.

5. Desmella is reported in this paper on 21 fern host species collected within the tropics, *Hyalopsora* on 24 species, *Milesia* on 63 species, *Uredinopsis* on 10 species, *Puccinia* on one species, and *Uredo* on 4 species. The paper lists a total of 109 tropical fern species (exclusive of varieties, etc.) known to be hosts of rust fungi; of these 73 are recorded for the first time.

6. I have found 25 rusted fern host species in Guatemala, 27 in Jamaica, 27 in tropical Mexico and 9 in Panama. Hashioka, in collections made both north and south of the Tropic of Cancer, reported 16 from Formosa (as published by Hiratsuka & Hashioka in their "Uredinales collected in Formosa"). Varieties are not included in any of these numbers, nor are the submarginal species of *Pteridium aquilinum*.

7. According to my experience, rusted ferns in the tropics are rarely found below an elevation of about 2000 feet above sea level. *Uredo* rust on *Lygodium* is exceptional; I collected it at sea level around Puerto Barrios in Guatemala. I could find no fern rusts on Barro Colorado Island, Panama Canal Zone; the greatest elevation on that island is said to be under 550 feet.

8. Much is to be expected from the vast mountainous regions extending eastward from Iran (Persia) to the South China Sea, from which have

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come scant collections only, and these from very limited northern areas, probably in reality extratropical, such as around Kunming, Yunnan, China. 9. Comprehensive data based on old and new records embodied in fern rust collections from the tropics are summarized in Table III. This table designates all the relevant fern genera hosts, the numbers of their affected species, the involved rust genera for each fern genus, and the regions in which the collections were made.

TABLE III

FERN RUST HOST GENERA IN THE TROPICS AND THEIR DISTRIBUTION

		Desmella	Hyalopsora	Milesia	Uredinopsis
Adiantum	4ª	Trinidad 1ª	Mexico 1; Brazil	1	Guatemala 1
Anemia	4	Brazil 3; Jam. 1; Mex. 1		Jamaica 1; Mexico 1	
Anogramma	1		Mexico 1		Mexico 1
Antrophyum	1		Dom. Rep. 1; Porto Rico 1		
Asplenium	2		Guatemala 1; Mexico 1	New Guinea 1	
Athyrium	4		Mexico 2; New Guinea 1	Mexico 1	Guatemala 1; Mexico 1
Blechnum	6	Brazil 1	Borneo 1	New Guinea 1 ^b ; Trop. Am. ^c 1, 1, 3	
Cheilanthes	4		Mexico 1	Jamaica 1; New Guinea 1	Mexico 1, 1
Coniogramme	1			Formosa 1	
Cyathea	4		New Guinea 1	Guatemala 1; Jamaica 1; Mexico 1	
Cyclopeltis	1	Trinidad 1			
Cystopteris	1		Mexico 1		Mexico 1
Dennstaedtia	6	Jamaica 1; Porto Rico 1		Colombia 1; Cuba 1; Guatemala 1; Jamaica 3; Mexico 2; Panama 1	
Diplazium	4	Cuba 1	New Guinea 2	Guatemala 1	

* The numerals indicate the number of host species involved. Those in black face are new records.

^b This might be a Hyalopsora.

^c Colombia 2, Costa Rica 1, Cuba 1, Ecuador 1, Guatemala 1, Jamaica 1, Mexico 2, Panama 1, Porto Rico 1, Venezuela 2.

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TABLE III (Continued)

		Desmella	Hyalopsora	Milesia	Uredinopsis
Dryopteris	29	Jamaica 2; Mexico 1; Porto Rico3; Venezuela 2	Guatemala 1	Ecuador 1, 2; Formosa 2; Guatemala 8; Jamaica 1, 9; Mexico 3; New Guinea 1; Panama 4	
Elaphoglossum	4		Colombia 1; Jamaica 1, 1	Mexico 1	
Gleichenia (?)	1			New Guinea 1	
Hemionitis	1			Jamaica 1	
Lygodium	4^{d}				
Nephrolepis	3			Colombia 1; Phil. Islands 1; Porto Rico 1	
Odontosoria	1			Jamaica 1	
Onychium	1			Phil. Islands 1	
Pellaea	3		Ecuador 1; Mexico 1	Madagascar 1	Mexico 1
Pityrogramma	2	Ecuador 1; Jamaica 1; Venezuela 1			
Polybotrya	1			Jamaica 1	
"Polypodiacea"	1	Ecuador 1			
Polypodium	7	Jamaica 1; Panama 1	Guatemala 3; Mexico 2	Formosa 1	Guatemala 1; Mexico 1
Polystichum	2			Formosa 1; Guatemala 1	
Pteridium					Almost world-wide
Pteris	2	Jamaica 2		Jamaica 1; Panama 1	
Tectaria	1			New Guinea 1	
Woodsia	1		Mexico 1		

^d Brazil 2; Br. Guiana 1; Guatemala 1; San Salvador 1; Trinidad 1; Venezuela 1. The rusts involved are referred to the genera *Uredo* and *Puccinia* in Tables I and II.

ARNOLD ARBORETUM,

HARVARD UNIVERSITY.